

3 FOOD WEBS

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THIRD FISHERMAN: Master, I marvel how the fishes live in the sea.

FIRST FISHERMAN: Why, as men do a-land — the great ones eat up the little ones.

Pericles, Prince of Tyre, Act 2

INTRODUCTION

The first ecologist to publish a diagram of a food web appears to have been V. E. Shelford in *Animal Communities in Temperate America*, published in 1913. The first to grasp the full theoretical significance and importance of food webs was Charles Elton in *Animal Ecology*, in 1927. The term 'food chain' is Elton's; his 'food cycle' we now refer to as a food web, that is a collection of food chains. It is worth quoting what Elton wrote over 60 years ago at some length, because much of it seems to have been forgotten:

... animals have to depend ultimately upon plants for their supplies of energy, since plants alone are able to turn raw sunlight and chemicals into a form edible to animals. [p. 56]

The herbivores are usually preyed upon by carnivores, which get the energy of the sunlight at third-hand, and these again may be preyed upon by other carnivores, and so on, until we reach an animal that has no enemies, and which forms, as it were, a terminus on this food cycle. There are, in fact, chains of animals linked together by food, and all dependent in the long run upon plants. We refer to these as 'food-chains', and to all the food-chains in a community as the 'food-cycle'. Starting from herbivorous animals of various sizes, there are as a rule a number of food-chains radiating outwards, in which the carnivores become larger and larger, while the parasites are smaller than their hosts. [pp. 56–57]

Size has a remarkably great influence on the organisation of animal communities. ... A little consideration will show that size is the main reason underlying the existence of ... food chains, and that it explains many of the phenomena connected with the food-cycle. There are very definite limits, both upper and lower, to the size of food which a carnivorous animal can eat. [p. 59]

Each stage in an ordinary food-chain has the effect of making a smaller food into a larger one, and so making it available to a larger animal. But since there are upper and lower limits to the size of animals, a progressive food-chain cannot contain more than a certain number of links, and usually has less than five. [p. 61]

If you make a list of the carnivorous enemies and of the parasites of any species of animal, you will see . . . certain curious facts about the sizes of the two classes of animals relative to their prey or host. . . . In fact, most animals have a set of carnivorous animals much larger than themselves, and a set of parasitic enemies much smaller than themselves . . . In all these cases we are, of course, speaking of the size relative to their prey or host. [pp. 71–72]

Apparently there are never very many stages in such food-chains of parasites. The reason for this is that the largest parasite is not very big, and any hyperparasite living on or in this must be very much smaller still, so that the fifth or sixth stage in the chain would be something about the size of a molecule of protein! [p. 78]

. . . the smaller an animal the commoner it is on the whole. . . . To put the matter more definitely, the animals at the base of a food-chain are relatively abundant, while those at the end are relatively few in numbers . . . Finally, a point is reached at which we find a carnivore . . . whose numbers are so small that it cannot support any further stage in the food-chain. [p. 69]

When we are dealing with a simple food-chain it is clear enough that each animal to some extent controls the numbers of the one below it. . . . Ultimately it may be possible to work out the dynamics of this system in terms of the amount of organic matter produced and consumed and wasted in a given time. . . . The effect of each stage in a food-chain on its successor is easy to understand, but when we try to estimate the effect of, say, the last species in the chain upon the first, or upon some other species several stages away, the matter becomes complicated. If A keeps down B, and B keeps down C, while A also preys on C, what is the exact effect of A upon C? [pp. 120–121]

These eight short paragraphs contain most of the essential ideas round which modern research on food webs is now focused, and some which have been lamentably ignored by Elton's successors. Food chains are energy transformers, supported ultimately by green plants. Body size offers a key to understanding structure in food webs, and so do dynamic interactions between species. Ecologists must study parasites as well as true predators when drawing up food webs.

Although not couched in the form of explicit hypotheses, there are also two explanations here for why food chains are short. The length of food chains is limited by constraints on species body sizes, and/or by the diminishing availability of food (energy) at successive steps in the chain. Elton obviously thought that both mechanisms were important.

We will have cause to return repeatedly to Elton's insights throughout this essay.

General remarks and organization

Food webs are diagrams depicting which species in a community interact. Obviously, the interactions are trophic, not competitive or mutualistic, although these distinctions are sometimes blurred. Published webs usually depict binary relationships — whether the species interact or not — and ignore a great deal of important biology, for

example the frequency and intensity with which species A feeds on species B. In Pimm's words (1982), most published webs are therefore 'caricatures of nature'. My dictionary defines caricature as a representation exaggerated for comic effect, or a ludicrously inadequate or inaccurate imitation! This is a fair assessment of most of the published information on food webs.

Confronted with limited data of highly variable quality, hardly any of which is really good, food web studies face either hand-wringing paralysis, or cautious efforts to see what can be discovered in the existing information. If nothing else, the latter course of action should serve as a spur to gather more and better data, particularly if published webs reveal evidence of interesting regularities and patterns in nature. However, we have to accept that some of the patterns may eventually prove to be artefacts of poor information. Bearing in mind this considerable worry, I have nevertheless chosen to adopt an optimistic approach, and first summarize evidence for the existence of ten patterns in the structure of published webs. There then follows a major section on theoretical explanations put forward to explain them. Patterns and explanations are gathered together for ease of reference in Table 3.1. The final parts of the paper review problems in the published data, and point to significant gaps in our knowledge.

PATTERNS

Patterns define positional relationships between species in a food web that recur more often than expected by chance. Current interest in patterns in food webs stems primarily from the publication of two books; Cohen's *Food Webs and Niche Space* (1978) and Pimm's *Food Webs* (1982). Ecologists now have 113 webs compiled from the literature (Briand & Cohen 1987) from which to seek evidence of non-random, non-trivial patterns in binary links between components of the web. Raking and reraking these published entrails is a small growth industry. As explained in the Introduction, I want first to summarize the patterns that have emerged from these analyses, without questioning the validity of the data on which they are based. Later, I want to discuss the quality of the information. One feature of the data that we do need to note here is the fact that many of the components of published webs are not single species; they may be genera, groups of similar taxa (e.g. 'herbivorous gastropods' or 'algae'), or incredibly heterogeneous organisms that happen to feed roughly in the same way [one such group, by no means atypical, consists of dragonflies, spiders and passerine birds! (Teal 1962; web 24 in Cohen 1978)]. For simplicity, it is conventional to refer to all

such groupings as 'species', even though we know it is an oversimplification.

The published patterns can be grouped under ten headings. This is not an exhaustive list; rather it contains those that seem to me to be the most interesting. They are:

- (i) A miscellaneous group that distinguishes real food webs from models where interactions are placed entirely randomly. These include a restriction on loops of the kind: species A eats species B eats species C eats species A etc. [termed 'acyclicity' by Gallopín (1972)], and absurdities such as predators without prey (Pimm 1982; Pimm & Lawton 1983). In the analyses that follow I have largely ignored biological absurdities; most of them are trivially obvious. I have, however, commented on feeding loops, because despite assertions to the contrary, under some circumstances these can, and do, occur in real food webs.
- (ii) On average each species feeds on a constant number of others, irrespective of the total number of species in the web (MacDonald 1979). Cohen & Newman (1985) call this property d the 'density of links per species'. As a consequence, as the number of species in the web increases, 'connectance', defined as the number of realized links, divided by the possible links, declines hyperbolically (Rejmanek & Stary 1979; Yodzis 1980; Pimm 1982; Cohen, Newman & Briand 1985).
- (iii) 'Top' species have no predators: 'intermediate' species serve as predators and prey; 'basal' species are prey. Then, the average proportions of basal, intermediate and top species in published webs are constant and independent of the total number of species in the web (Briand & Cohen 1984; Cohen & Briand 1984). Based on an entirely different, taxonomically more reliable data set, but using a cruder trophic classification, Jeffries & Lawton (1985) found that the ratio of predator species to prey species in freshwater communities was roughly constant, and independent of the number of species in the sample. Similar observations have been made by others (e.g. Evans & Murdoch 1968; Arnold 1972; Cameron 1972; Moran & Southwood 1982).
- (iv) Perhaps not surprisingly, given (ii) and (iii), the average proportion of links between basal, intermediate and top species is also independent of the number of species in the web, although variation round this average trend is large (Cohen & Briand 1984).
- (v) In the food web literature, an 'omnivore' is a species that feeds on more than one level in the food chain. In published food webs, omnivores are rarer than expected (Pimm & Lawton 1978, 1983; Pimm 1982), which may be more or less the same as Cohen & Briand's (1984) observation that most published webs lack feeding links between basal

and top species. There are, however, some apparent exceptions to this generalization, for example, webs of insects and parasitoids often show abundant, and very complex patterns of omnivory (Pimm & Lawton 1978, 1983; Pimm 1982), as may assemblages of decomposers (Pimm 1982; Pimm & Lawton 1983). However, perhaps more than any other pattern, the real extent of omnivory in food webs may be seriously distorted by poor-quality and highly aggregated data (see, for example, the discussions in Sprules & Bowerman 1988). Patterns of omnivory therefore require particularly careful interpretation.

(vi) Webs from 'fluctuating' and 'constant' environments differ. Webs from constant environments have proportionately more links between basal and top species [i.e. more omnivory in the sense of pattern (v)] than webs from fluctuating environments, and show greater variance in many characteristics, for example in proportions of links (pattern iv) and species (pattern iii) in various trophic positions (Briand & Cohen 1984; Cohen & Briand 1984). Webs from fluctuating environments also appear to have lower connectance (Briand 1983; Cohen, Newman & Briand 1985).

(vii) Food chains are short (Elton 1927; Hutchinson 1959; Pimm & Lawton 1977). Typically the modal number of species between the base and top of published webs is three or four; six species or more is very rare (Pimm 1982). Two additional points are worth making at this juncture. First, here and throughout the chapter, I have tried to avoid the term 'trophic level'. It is practically impossible to assign many real species to fixed trophic levels, and the concept conceals more than it reveals (Darnell 1961; Cousins 1980, 1987; Platt 1985). Second, although it is a familiar idea that food chains are short, this particular pattern depends on the way in which steps are defined. Food chains are short only if detritus and bodies are regarded as the start of a new chain (Patten 1985).

(viii) Habitat structure influences the length of food chains, which appear to be shorter in 'two-dimensional' habitats (e.g. grassland) than in 'three-dimensional' (e.g. forest) or 'solid' (e.g. pelagic) habitats (Briand & Cohen 1987).

(ix) Theoretically, webs are said to be divided into 'compartments' when the majority of interactions between species take place within blocks or modules of species, and there are very few interactions between blocks. Published webs based on binary links between species are not divided into compartments within habitats, but evidence for compartments can be found at habitat boundaries (Pimm & Lawton 1980; Pimm 1982).

(x) Food webs are 'interval' more often than expected by chance (Cohen 1977, 1978, 1983). Basically, this property of webs describes patterns of

overlap in prey use by predators. If overlaps can be expressed in one dimension, the web is interval; if it requires two dimensions to illustrate the pattern of overlap between predators, the web is non-interval. This somewhat abstract property of food webs is described further on p.62.

EXPLANATIONS

Energy flow

The standard, text-book explanation maintains that food chains are short because energy transfer between links is inefficient. Eventually, there is too little energy to support another link in the chain (Hutchinson 1959). As we have seen, Elton (1927) believed this was one reason why food chains are short, and in the limit, the proposition is obviously true. To maintain a single predator at a trophic level higher than twenty requires an area of land bigger than some continents (Slobodkin 1961). But the energy hypothesis conspicuously fails to explain why food chains are as short as they are. More specifically, it predicts that food chains should be longer in more productive ecosystems (Pimm & Lawton 1977). Oksanen *et al.* (1981) present some data that may be consistent with this prediction; other studies are not (Pimm 1982). However, both these tests are based on limited information, and neither is definitive. Nor is the observation that food chains differ in length definitive even though energy inputs are very similar (Kitching 1983; Kitching & Pimm 1985; Pimm & Kitching 1987), although such data suggest that the length of food chains is determined by something other than energy flow.

The most comprehensive test of the hypothesis that food chains should be longer in more productive ecosystems is by Briand & Cohen (1987). They found no difference in food chain length comparing twenty-two published webs from habitats with a mean productivity less than 100 g of carbon $\text{m}^{-2} \cdot \text{year}^{-1}$, with ten webs in which productivity exceeded 1000 g of carbon $\text{m}^{-2} \cdot \text{year}^{-1}$, and six webs from intermediate habitats. It is remarkable that other, similar tests have not been attempted based on good, new data on the structure of food webs along gradients of productivity. It is equally remarkable that manipulative, experimental tests have also been so slow to emerge. A pioneering attempt has now been made by Pimm & Kitching (1987). I admire their idea, but have reservations about what the results tell us.

Pimm and Kitching created small, artificial analogues of water-filled tree holes, sustained by a supply of leaf litter, in a Queensland rain forest

where similar natural tree holes abound. They varied 'productivity' by setting litter inputs from half to twice the natural rates, a four-fold range, and argued that because 'the percentage of energy consumed that goes into new tissues is between 20 and 50% in short-lived ectotherms like insects' (typical tree-hole inhabitants), an extra trophic level is expected between the least and the most productive containers. I disagree. It is not production/consumption ratios for invertebrates that lie in the range 0.2–0.5, but ratios of production/assimilation (McNeill & Lawton 1970; Humphreys 1979). Hence to energy losses measured by the ratio of production to assimilation must also be added food that is consumed and not assimilated *plus* energy made available by production in the previous trophic level that is not consumed by the next. In other words, what matters is the overall 'ecological efficiency' of energy transfer between steps in the food chain, and as Slobodkin (1961) showed long ago for small aquatic invertebrates, this efficiency is unlikely to be much better than 10%. In consequence, I would not expect a four-fold range in productivity to extend the length of tree-hole food chains by more than an average of about 0.4 of a step. Pimm and Kitching did not find longer food chains developing in their more productive containers, and claim that this result is inconsistent with the energy hypothesis. That may be so, but it may also be that they did not vary energy inputs enough to see an effect. The result is therefore equivocal. These experiments are being repeated using a wider range of productivities (S.L. Pimm, personal communication); the results will be fascinating.

Consideration of ecological efficiencies permits an alternative test of the energy flow hypothesis. Endothermic animals have much lower ecological efficiencies than invertebrate ectotherms (about an order of magnitude less; Lawton 1981). Hence, for a given level of energy input, food chains of ectotherms should be longer than endotherm chains (Pimm 1982). Some clever accounting by Yodzis (1984a) based on thirty-four published food webs suggests that this is indeed the case. The number of additional links in food chains supported by vertebrate endotherms is significantly less than the number of additional links supported by invertebrate ectotherms; vertebrate ectotherms are intermediate both in ecological efficiency and in the number of additional links which they support. Yodzis' intriguing result stands as sole support for the hypothesis that food chains are short because of energetic constraints. It is not easily reconciled with Briand & Cohen's (1987) analysis, and at the moment serves to highlight how little we really know about so fundamental an ecological problem.

*Dynamic constraints**Predictions derived from Lotka-Volterra models*

Simple Lotka-Volterra models of food webs can be used to make a number of predictions about structure. The rules are straightforward. To mimic the real world, model food webs must be feasible (all populations with positive equilibria) and locally stable (returning to equilibrium after small perturbations), because (ignoring locally unstable, but persistent solutions, for example limit cycles) structures and parameter values that lead to non-feasible, unstable models will be transitory, rare or absent in the real world (Yodzis 1981; Pimm 1982). These simple dynamic constraints generate several patterns in model food webs that are also common in real webs (Table 3.1). They include a general lack of omnivory except in insect webs (Pimm & Lawton 1978; Pimm 1979); low connectance and an upper bound between connectance and species richness that declines hyperbolically as the number of species in the web increases (May 1972); reticulate webs that are more stable than compartmented webs (Pimm 1979, 1982), [although theoretical views on this point are contradictory, e.g. May (1972, 1979); O'Neill *et al.* (1986)]; and an approximately constant ratio of predator species to prey species (Mithen & Lawton 1986). Adding one more dynamic constraint to the modelling process, namely that populations with the ability to return rapidly to equilibrium after a disturbance are more likely to persist in the face of repeated environmental shocks, leads to a further prediction. Long food chains have long return times; hence food chains in the noisy real world must be short (Pimm & Lawton 1977), and should be shorter in more variable environments. Finally, elaborating Lotka-Volterra models to incorporate the effects of age and size/structure (Pimm & Rice 1987) reconfirms the destabilizing effects of omnivory, and finds that feeding loops (A eats B eats C eats A) are strongly destabilizing. Both omnivory and loops are more likely on natural history grounds if members of a food web change markedly in size during development, and feed on different things as they grow (e.g. Hardy 1924; Darnell 1961).

By inference, the more variable structure, greater connectance and more extensive omnivory shown by webs from constant environments may also be a product of more stringent dynamic constraints for persistence and stability in fluctuating environments (May 1981, 1986; Briand 1983), although there have been no formal tests of this possibility, for example by modelling Lotka-Volterra food webs in a stochastic environment. Last but not least, simple dynamic constraints do not

TABLE 3.1. Summary of patterns found in published food webs, together with a list of theoretical explanations advanced to explain the patterns. ● signifies that theory predicts the observed pattern; ○ signifies that it does not. A blank cell denotes that no attempt has been made to link that combination of pattern and theory. Parentheses signify tentative or uncertain predictions. (See text for further details)

Theoretical explanations	Observed patterns									
	i	ii	iii	iv	v	vi	vii	viii	ix	x
	Feeding loops absent	Links per species constant. Connectance declines hyperbolically with increasing number of species	Constant proportion of basal, intermediate and top species (constant predator/prey ratio)	Constant proportion of links between basal, intermediate and top species	Omnivory rare, except in insect-parasitoid and donor controlled webs	Webs from constant environments have more connectance, more variation and more omnivory	Food chains are short	Food chains shorter in 2-dimensional habitats	Webs are not compartmented except at habitat boundaries	Food webs are interval
Energetic constraints							(●)			
Standard dynamic models in Lotka-Volterra form	●	●	●		●	(●)	●		●	○
Donor controlled dynamics		○			●		●			
Neutral interactions (no dynamics; links assigned randomly, subject to minimal biological constraints)					○		(○)			(○)
Cascade model generated by body-size constraints (no dynamics)	●	Assumed by model	●	●	(○)		●			(●)
Natural history, optimal foraging and other evolutionary constraints		●			●		(●)		●	

appear to explain why food webs are predominantly interval (Cohen 1978), although this problem has not been particularly well explored (see, for example, Pimm 1978, 1982 and Cohen 1983).

Drawing these arguments together, an impressive proportion of the patterns seen in real food webs enhance the stability of model webs, with the reasonable inference that real webs are strongly, though not entirely structured, by similar dynamic constraints (Pimm 1982; Pimm & Lawton 1983). Given that a central aim of science is to explain as much as possible about nature with the minimum number of assumptions, this is an exciting result. It has a level of elegance and generality that is all too rare in ecology. But elegant results are not necessarily true. There are two problems; first, the models may be making the right predictions for the wrong reasons, and second, there may be alternative ways of generating the same patterns. Next, I review a limited number of independent tests of the dynamic constraint hypothesis, before moving on to consider problems in the assumptions that underpin the Lotka–Volterra models. Alternative explanations for food web patterns follow in later sections.

Independent tests of model predictions

Schoener & Spiller (1987) show how dynamic constraints in real food webs may eliminate species and reduce omnivory, although this was not the purpose of the original experiment. On Caribbean islands, spiders prey on small insects and are themselves eaten by lizards. The lizards are omnivores in the sense of Pimm & Lawton (1978) because they too feed on small insects. Experimentally removing lizards greatly enhanced spider density and diversity; in the presence of lizards this middle trophic level was much reduced because not only were spiders preyed on by lizards, but they also competed with them for insect prey, exactly as the models predict (Pimm 1982). In other words, omnivory in real systems may be rare, because intermediate species are squeezed out of the food chain. In the case documented by Schoener and Spiller, only some species of spiders suffered this fate, but the general mechanism is well illustrated.

The only prediction arising from Lotka–Volterra models of food webs that has been subject to explicit, independent tests is the argument that food chains should be shorter in more variable environments. Although Briand & Cohen (1987) find that this is indeed the case, their sample of food webs confounds environmental variability and habitat structure, and they conclude that when the latter is factored out, constant environments do not support markedly longer food chains. My own view is that assigning webs to ‘constant’ or ‘fluctuating’ environments in

Briand and Cohen's compendium is so subjective (based on the impressions of the original authors who drew up the webs), and sample sizes are so small when habitat structure has been factored out, that no firm conclusions can be drawn. This is a classic case of a clever idea being frustrated by a shortage of suitable data; criticism is easy, but doing anything better is not!

The same water-filled tree holes that provided a test of energetic constraints on food chain length also provide a test of dynamic constraints. Although total energy inputs in the form of leaf litter are very similar in tree holes in England and Queensland, inputs are spread more constantly over the year in Queensland where climatic fluctuations are less. As predicted, food chains are shorter in English tree holes (Kitching 1983). Similar empirical observations on a wide range of 'phytotelmata' are made by Kitching & Pimm (1985), who conclude that variations in 'spatial and temporal uncertainty' are a major contributor to differences in food chain lengths in these particular systems. Moreover, species feeding higher in the food chain also recruited more slowly than lower levels after an experimental disturbance to the Queensland system (Pimm & Kitching 1987). A reasonable inference is that frequent disturbances make it impossible for high ranking carnivores to persist in the community. But it is not reasonable to conclude that these observations test and vindicate simple Lotka-Volterra models of food webs. The problem is that Pimm and Kitching's result is also consistent with an alternative dynamic model (see p. 57). It is to this, and other alternatives that we must now turn.

Problems with Lotka-Volterra models

Why use them at all?

Ecologists mistrustful of mathematics have frequently pilloried the use of simple models in ecology, I have no intention of rehearsing these arguments here. However, all models make assumptions, and in the present context some of these assumptions make a big difference to 'permitted' structures in model food webs, and need to be confronted.

This is not to say that I regard the existing models as a waste of time. Fifteen or 20 years ago, food web theory had progressed very little since Elton (1927), and interest in developing such theory was moribund; food webs were about energy flow, and that was that. There were a few fascinating exceptions to this otherwise lack-lustre field, for example MacArthur (1955), Elton (1958), Paine (1966, 1969) and May (1972,

1973). But the idea that there might be regular patterns in the structure of food webs was not part of the intellectual baggage of most ecologists. If they thought about the problem at all, they most probably subscribed to what Stuart Pimm and I privately referred to as the 'tangled knitting hypothesis' of food web structure; you can sometimes see interesting shapes, but unravelling them is impossible. It therefore seemed worth while to strike out in a new direction and discover whether population dynamic interactions between species could generate simple rules constraining the structure of food webs, and to seek evidence for dynamic constraints in the real world.

In reality, the idea was not that new. As we have already observed, Charles Elton clearly recognized the potential importance of dynamic interactions between species in food webs in 1927. Returning to the theme in *The Ecology of Invasions by Animals and Plants* (1958), he explicitly discusses the possibility of modelling interactions between species in a food chain using Lotka–Volterra equations (pp. 130–131) (cautioning, however that such models are 'oversimplified'). Of course they are simplified, but as in all science, it is often interesting to see what progress can be made with the minimum number of assumptions. The results of this adventure are summarized in Pimm (1982), who provides a bold, lucid and internally highly consistent review. Now the dust has settled, my own view is that simple Lotka–Volterra models get some of the answers right for more or less the right reasons; and some they get right for quite the wrong reasons. These arguments will become clearer as we proceed.

Interaction strength, closely coupled enemy–victim interactions, spatial heterogeneity and other assumptions

There are a number of important ways in which the predictions of simple Lotka–Volterra models of food webs can be altered by making different assumptions, or by using rather different models. For example, combining population dynamic and energy flow constraints in one model alters the prediction that high connectance necessarily creates instability (DeAngelis 1975; Kirkwood & Lawton 1981). Or consider the hypothesis, based on return-times, that long food chains are dynamically fragile. As May (1981) points out, this prediction hinges on some subtle mathematics; Pimm (1982, 1984) assembles arguments in its defence. The problem is that alternative models give contradictory signals. Difference equation models of insect host–parasitoid–hyperparasitoid interactions bolster the conclusion that long food chains are dynamically fragile, based on familiar local stability criteria rather than more

contentious return-time arguments (Beddington & Hammond 1977). In contrast, DeAngelis *et al.* (1978) and DeAngelis (1980) show that long food chains may still be stable, providing the transit time for a molecule or unit of energy through the web is fast. An obvious corollary of this work is that species of small body size, with short generation times and high weight-specific metabolic rates (Peters 1983), should build up longer food chains than large-bodied species. The difficulty is that body size is implicated in food web structure in other, much simpler ways, making the argument a difficult one to test.

Over and above these specific examples are two much more general and serious problems. The first is the assumption that links in food webs all involve closely coupled enemy–victim interactions; the second is that the interactions take place in a spatially homogeneous world. It is inconceivable that both assumptions are always met in the sample of published food webs that ecologists have used to determine patterns in nature; they are probably approximately true for some of the links. Yet changing either assumption changes the predictions of food web models, making it hard to avoid the conclusion that for a significant, but unknown, proportion of real food webs, simple Lotka–Volterra models are making the right predictions for the wrong reasons.

Pimm (1982) argues forcefully that predators usually affect the dynamics of prey populations. Hence models in which predators affect prey populations and prey populations in turn influence predator dynamics (the classical, closely coupled Lotka–Volterra assumptions) are appropriate descriptions of the real world. Nobody denies that enemies can and do significantly influence the population dynamics of myriads of victim species (e.g. Huffaker 1971; Strong, Lawton & Southwood 1984; Sih *et al.* 1985, Carpenter *et al.* 1987), and that many food webs contain examples of strong interactions involving ‘keystone’ predators (Paine 1966, 1969, 1971, 1980; Krebs 1985; Menge & Sutherland 1987). But common sense and data both suggest a continuum of possibilities. At one extreme are closely coupled enemy–victim interactions; at the other are totally neutral feeding links of no consequence for the dynamics of either consumer or consumed. Between them are two possibilities, namely ‘donor controlled’ dynamics in which victim populations influence enemy dynamics but enemies have no significant impact on victim populations, and the alternative in which enemies influence victim populations, but not vice-versa. (This latter possibility may occur with very polyphagous predators, where individual species of prey have trivial effects on the predator’s dynamics. The problem has received no attention in the food web literature, and will not be considered further

here.) To some extent, Lotka–Volterra models that sample from a range of possible parameter values, embracing highly efficient as well as ineffective predators (e.g. Pimm & Lawton 1977, 1978; Pimm 1982; Mithen & Lawton 1986) may allow for all these possibilities. But my feeling is that in general, such models still give too much emphasis to tightly coupled enemy–victim interactions.

Consider donor control first. There are technical problems in designing field experiments that are both powerful enough and on the right spatial and temporal scales to detect significant predator impacts on some victim populations (e.g. Carpenter & Kitchell 1987; Johnson *et al.* 1987), but even with this caveat, donor controlled dynamics do not appear to be unusual. A familiar example is consumers in decomposer food chains that may have no influence on the rain of plant material and animal bodies that sustains them (Pimm 1982). Odum & Biever (1984) provide several other examples, including nectarivores and possibly many seed feeders. It seems extremely unlikely that many rare phytophagous insects, whose species are legion, have any impact upon the abundance of their host plants (Caughley & Lawton 1981; Strong, Lawton & Southwood 1984). Biological control agents frequently establish, but fail to have any measurable impact on the target pest (e.g. Kelleher & Hulme 1984; Hokkanen 1986). Parasitoids and predators of insects in more natural situations may display dynamics that appear to be predominantly donor controlled (Dempster & Pollard 1981). Evidence for significant top down control is also conspicuous by its absence in many freshwater food chains (Harris 1985; Thorp 1986). Even the classical food chain from trees to caterpillars, small birds and sparrowhawks appears to be donor controlled at the link between small birds and hawks; ‘there is no good evidence of sparrowhawks having a widespread effect on the breeding numbers of their prey, (however) there is circumstantial evidence for the reverse, that sparrowhawk numbers are affected by prey numbers’ (Newton 1986). The ‘circumstantial’ evidence, incidentally, is impressive.

In the limit, we must expect many documented feeding links in food webs to have trivial consequences for both enemy and victim. Paine (1980, 1983, 1988) provides some of the best examples (see also Menge & Sutherland 1987). One problem is that the population dynamics literature is undoubtedly biased towards ‘significant’ enemy–victim interactions. If newspapers were our sole source of information about society, we could imagine that people spend most of their time in highly unpleasant, exciting and strong interactions with one another. The reality is that for most of us, most of the time, life is humdrum; no news may be good news, but it doesn’t sell papers. The extent of a similar bias in the

ecological literature is hard to gauge, but it is undoubtedly there. However, in drawing up a food web, there is at least the opportunity to illustrate links that nobody seriously believes would be interesting to study in their own right. The problem is that there are no agreed criteria for what constitutes a significant link (May 1983, 1986; Paine 1988). Common sense suggests that only some of the links in published webs are best modelled by closely coupled enemy-victim interactions, or by donor control, and that many have trivial dynamic consequences.

The last, crucial assumption in the simple models is that encounters between enemy and victim populations take place at random in a spatially uniform world. In reality, most populations have clumped distributions, and many (though by no means all) predators and parasitoids search non-randomly and aggregate their attacks on the high density patches (e.g. Hassell 1978; Lessells 1985). Herbivores may behave in a similar manner (Kareiva 1983; Strong, Lawton & Southwood 1984).

Effect of changing the assumptions on model predictions

Compared with standard Lotka-Volterra models, donor controlled interactions have very different dynamics, and make very different predictions about web structure (Pimm 1982). There are no longer tight constraints on overall connectance (DeAngelis 1975), and rampant omnivory is not destabilizing. It is unclear how other food web patterns are affected. Intriguingly, preliminary evidence suggests that omnivory may be common in some decomposer food webs (Macfadyen 1979; Pimm 1982; Pimm & Lawton 1983; Walter 1987), where we expect to find donor control. This apparent pattern is crucial to the present arguments and deserves more attention.

Species feeding high in the food chain of a donor controlled system must still be vulnerable to stochastic extinction, simply because they will have smaller populations than more basal species (Leigh 1981; Fowler & MacMahon 1982). Hence experiments or observations showing that food chains are shorter in more unpredictable environments (see above) are consistent with both donor controlled models of food webs, and predictions based on standard Lotka-Volterra equations, and cannot be used to distinguish between them.

If feeding links are dynamically trivial, species can be assembled in food webs free of any dynamic constraints. Below, we shall explore models of food web assembly free of dynamic constraints, but with other limitations. Here I want to restrict attention to cases where assembly is virtually a free for all. The outcome is rather unsatisfactory; model food

webs with links assigned at random, subject to minimal, biologically sensible constraints appear to have too many trophic levels and too much omnivory compared with real webs (Pimm 1980a, 1982), and may also be non-interval more often than real webs (Cohen 1978). Unfortunately, both studies are not without problems, and require cautious interpretation (Pimm 1978; Cohen, Briand & Newman 1986).

Yodzis (1984b) attempts a similar exercise, assembling food webs without dynamics, but subject to the rules of ecological energetics. He shows that it is possible to construct food webs that match many of the properties of forty real webs gathered together by Briand (1983), particularly for webs from fluctuating environments. However, I have serious reservations about this result. First, the assembly process terminates abruptly when energy availability at the top of assembled food chains falls below an arbitrary value; without such a rule, the simulated food chains would be too long. Second, concordance between real webs and their model counterparts is obtained by varying primary productivity and ecological efficiency. Although the ranges of parameter values used for both are defensible (though ecological efficiencies tend to be rather low), it is unclear how they were selected to simulate individual webs. The primary productivities, in particular, bear no resemblance to actual productivities, where these are known for particular webs (compare values in table 1 in Briand & Cohen 1987, with those in table 1 of Yodzis 1984b). Accordingly, although the idea is interesting, I do not think that we learn very much that is useful from this particular analysis.

Worries about the effects of spatial heterogeneity on model predictions centre on cases where predators have a significant impact on prey populations. Spatially heterogeneous trophic interactions tend to be markedly stabilizing in a wide variety of population models (Hassell & May 1985; Chesson & Murdoch 1986; DeAngelis & Waterhouse 1987; Sih 1987). They have not been used to investigate properties of model food webs systematically, but some of their effects are not difficult to predict. For example, the standard Lotka-Volterra models used throughout Pimm's book incorporate 'self-damping' terms only at the base of food chains. Species higher in the trophic stack experience intraspecific competition via resource exploitation, but not via behavioural interactions, for example territoriality. Strong and effective self-damping is one way to produce donor control. The extent to which self-damping should be incorporated into model food webs has been debated by Saunders (1978), Lawton & Pimm (1978), Yodzis (1981) and Pimm (1982). These arguments focus on the significance of conventional intraspecific behaviours that lead to self damping, and by and large I believe they are correct to play down their importance in food web

dynamics. What they conspicuously overlook is the fact that predator aggregation and the differential exploitation of prey in high density patches generates dynamic effects that are identical to more familiar forms of intraspecific behavioural interactions between predators (Murdoch & Reeve 1987). For this reason, Free, Beddington & Lawton (1977) coined the term 'pseudo-interference' to describe them. Most of the theoretical work on pseudo-interference has been confined to insect host-parasitoid systems, although there is no reason to believe that parasitoids have a monopoly on the problem. Permitting predators in general to contribute to stability by incorporating aggregative responses into food web models is likely to lead to significantly more robust systems, although it may not alter many of the qualitative predictions generated by simpler models (May & Hassell 1981; Pimm 1982). The problem therefore remains open.

CASCADE MODEL AND BODY SIZE

An alternative major hypothesis

It should now be clear that although simple Lotka-Volterra models correctly predict the existence of a number of patterns in published food webs, the worry must be that they are giving us the right answers for the wrong reasons, at least sometimes. As Pimm (1982) remarks (p. 125), science is most interesting when there are at least two rival hypotheses consistent with published data. A series of papers by Joel Cohen and his colleagues provide one such rival hypothesis (Cohen & Newman 1985; Cohen, Newman & Briand 1985; Cohen, Briand & Newman 1986; Newman & Cohen 1986).

The hypothesis is a static model of the assembly of species into food webs; no dynamics are involved. Links are assigned essentially at random. But it differs in one crucial way from the static models of food web assembly outlined above, by imposing a simple constraint. The model assumes that species can be arranged *a priori* into a cascade or hierarchy such that a given species can feed on only those species below it, and can itself be fed upon by only those species above it in the hierarchy. Cohen and his co-authors refer to it as the cascade model. Precise details of the model, and the way in which it is used to generate predictions about food web structure are in Cohen & Newman (1985). Over and above the apparently arbitrary assumption of a trophic hierarchy, the model also makes one other key assumption. In order to use it to assemble model food webs, the density of links per species (d on p. 46) must be specified and fixed in advance. Cohen *et al.* use the

observed values in published webs, either an average over a sample of webs, or a single value from each web, depending upon their question. Hence the cascade model cannot say anything about pattern (ii) on p. 46, because it is already built into the model. We will return to this constraint on connectance later.

Food webs assembled according to this recipe have the correct proportions of basal, intermediate and top species, and the correct distribution of trophic links, except the cascade model tends to generate webs with too many links between basal and top species (Cohen & Newman 1985; Cohen, Newman & Briand 1985). It also gets close to predicting the lengths of most published food chains. However, there is a tendency for the model to create food chains that are too long (S.L. Pimm, personal communication; and see Cohen, Briand & Newman 1986), and it also tends to be wide of the mark in predicting chain-lengths for 16 or 17 webs in a total of 113 which have either an unusually high (more than four) or an unusually low (less than two) mean number of actual links (Cohen, Briand & Newman 1986). The length of food chains grows very slowly as increasing numbers of species enter the assembly process under the cascade model; even with a million species, the median number of links in the longest chain is below seventeen (Newman & Cohen 1986).

An excess of predicted over observed links between basal and top species is not necessarily the same as too much omnivory. Top species that feed both on basal species and intermediate species are omnivores. But chains of two species (a basal species fed on by a top species) cannot have omnivores. Accordingly, it is not possible to tell whether the excess of basal to top links in Cohen *et al.*'s simulated webs is due to too much omnivory, or to too many two-species chains. The cascade model may also obscure patterns of omnivory generated by links within the category of intermediate species, and between intermediate and top and intermediate and bottom species. Hence, although it is plausible that the cascade model predicts too much omnivory, this is by no means certain.

Why the cascade model? The role of body size

Cohen *et al.* offer no explanation for why species in food webs feed only on individuals below them in the hierarchy, and are themselves fed on only by individuals higher in the hierarchy. What determines the order of species? How is the hierarchy created? One simple possibility, unequivocally recognized by Elton over 60 years ago is body size (Warren & Lawton 1987; and see Paine 1963). As Elton points out, although it is not universally true, very commonly, predators are larger than their prey.

both in vertebrate (Gittleman 1985; Verezhina 1985) and in invertebrate (Warren & Lawton 1987 and references therein) food chains. The result is a trophic hierarchy based on body size, sufficient to conform to all the requirements of the cascade model. Plants at the bottom of the cascade reinforce its structure, as do detritus particles of a wide range of sizes (Cousins 1980, 1987). Limnologists and marine biologists have long recognized the importance of size in trophic interactions (e.g. Kerr 1974; Platt & Denman 1977; Harris 1985; Platt 1985 and references therein). The concept of a 'trophic continuum' in food webs, in which body size plays a crucial role has been most clearly developed by Cousins (1980, 1987). The only additional argument advanced by Warren & Lawton (1987) is to link these familiar effects of body size to the cascade model.

There are, of course, exceptions to the generalization that predators are usually larger than their prey, but they are revealing. Again as Elton pointed out, insect parasitoids and parasites in general are *smaller* than their hosts. Imagine a matrix with species listed along the rows and again down the columns. Non-zero elements in the matrix define the presence of feeding links between species. Technically, feeding links in the cascade model are 'upper triangular'; that is all the links lie above the leading diagonal of the matrix (see Cohen & Newman 1985 for further details). A food web matrix with species arranged from the smallest to the largest along the rows and down the columns will be strictly upper triangular if predators can feed only on species smaller than themselves (Warren & Lawton 1987). Parasitoids and parasites that can attack only species larger than themselves create food web matrices that are 'lower triangular', and the cascade model still holds (flipping a lower triangular matrix over round the main diagonal makes it upper triangular). Mixed food webs of parasites and 'real' predators may contain entries in the matrix above and below the main diagonal, and violate the assumptions of the cascade model. But in the published food web literature, mixed parasite and predator food webs are very rare. People either study 'real' predators, or food webs of insects and their parasitoids; they rarely study both (but see Hawkins & Goeden 1984), and hardly anybody incorporates parasites or diseases into food web diagrams (see below). Hence published food webs conform to the assumptions of the cascade model, based on a hierarchy of body sizes, not because there are no exceptions, but because nobody has really studied them.

Much the same may be said about obvious exceptions to the rule that predators are usually bigger than their prey. Group hunters, employing what Elton called 'flock tactics', are capable of overpowering prey much larger than themselves (hunting dogs, or driver ants for example). However, such predators are again conspicuous by their absence in

published food webs. In other words, a trophic cascade generated using body sizes will only describe a subset, albeit a major subset, of trophic links in real communities (Warren & Lawton 1987).

Intervality

Patterns of overlap in prey use by predators, sufficient to generate interval food webs are a possibility if feeding relationships are constrained by body size. If prey species increase in size from A to D, and predators increase in size from 1 to 3, the resulting food web is interval if predator 1 takes A and B, predator 2 takes B and C, and predator 3 takes C and D. Intervality is conserved with more overlap, providing, for example, that species 3 takes B, C and D, or indeed all four prey species. But the web is not interval if 3 feeds on A, C and D, but never on B. As Cohen (1978) points out, any food web in which at least one kind of prey is eaten by all predators is interval. In other words, a trophic cascade generated using body size as the ordering variable has the potential to produce interval food webs. However, a recent unpublished study (reported in Cohen & Newman 1988) finds that although food webs made up of small numbers of species, assembled according to the cascade model, have a high probability of being interval, this is not true of large webs. Nor is body size the only niche dimension capable of generating intervality (Cohen 1978; Sugihara 1983, 1984). The problem is therefore unresolved.

OTHER EXPLANATIONS

A rag bag of hypotheses and explanations for some of the observed patterns in published food webs may be brought together under the twin banners of natural history and optimal foraging. Natural history (a Jack of all trades is master of none) may constrain species to feed on only a limited number of others in the community, generating pattern (ii) (Pimm 1980b, 1982). If food webs are divided into compartments anywhere, it will be at obvious boundaries between habitats (Pimm & Lawton 1980; Pimm 1982). Omnivory may also be subject to simple biological constraints that are relaxed in detritus food chains; bodies don't bite back. Although patterns of omnivory do not seem to be entirely determined by simple natural history constraints (Pimm & Lawton 1978, 1983; Pimm 1982), a more recent and more thorough analysis by Yodzis (1984c) suggests that the difficulty of feeding simultaneously on both plants and animals is sufficient to account for the relative shortage of

omnivory in published webs. Probably all these simple natural history constraints contribute to observed patterns.

Finally, it has been suggested that obvious advantages may accrue to species by feeding as low in the food chain as possible, where resources are more abundant, whilst avoidance of competitors may favour being higher in the chain; the length of food chains reflects these counterbalancing selective forces (Hastings & Conrad 1979; Pimm 1982; Pimm & Lawton 1983; Stenseth 1985). The length of food chains may also be constrained by 'engineering' problems; a predator large enough to feed on eagles may not be able to fly (see Pimm 1982 for further discussions).

Habitat structure and the length of food chains

None of the theoretical explanations gathered in Table 3.1 explains Briand & Cohen's (1987) observation of shorter food chains in 'two-dimensional' habitats. One possibility is that structurally complex 'three-dimensional' habitats create prey refuges that either stabilize predator-prey interactions (Hassell 1978) or generate donor-controlled dynamics; both favour the persistence of long food chains. The problem is that 'solid' habitats, open water for example, also have long food chains, but lack structural complexity. A more fundamental worry is the arbitrary nature of the habitat classification based on human scales and perceptions. A prairie may look two-dimensional to a buffalo or a biologist, but it is anything but two-dimensional for a beetle. Habitat surfaces are fractal (Morse *et al.* 1985; Lawton 1986a), so that 'living space' must be defined according to the size(s) of the organism(s) under investigation. *A priori* it is difficult to see why Briand & Cohen's anthropocentric habitat classification generates anything very interesting. But obviously it does. Why is a mystery.

DISTINGUISHING BETWEEN EXPLANATIONS

Table 3.1 summarizes the theoretical arguments from the last section, and shows that most of the empirical patterns teased out of published food webs could be generated by more than one mechanism. Despite a strong historical association between food chains, trophic levels and energy flow, it is clear from Table 3.1 that ecological energetics has little to contribute to an understanding of structure in food webs, aside from the important question of whether energy flow or something else limits the length of food chains. There are no less than five plausible explanations for why food chains are short.

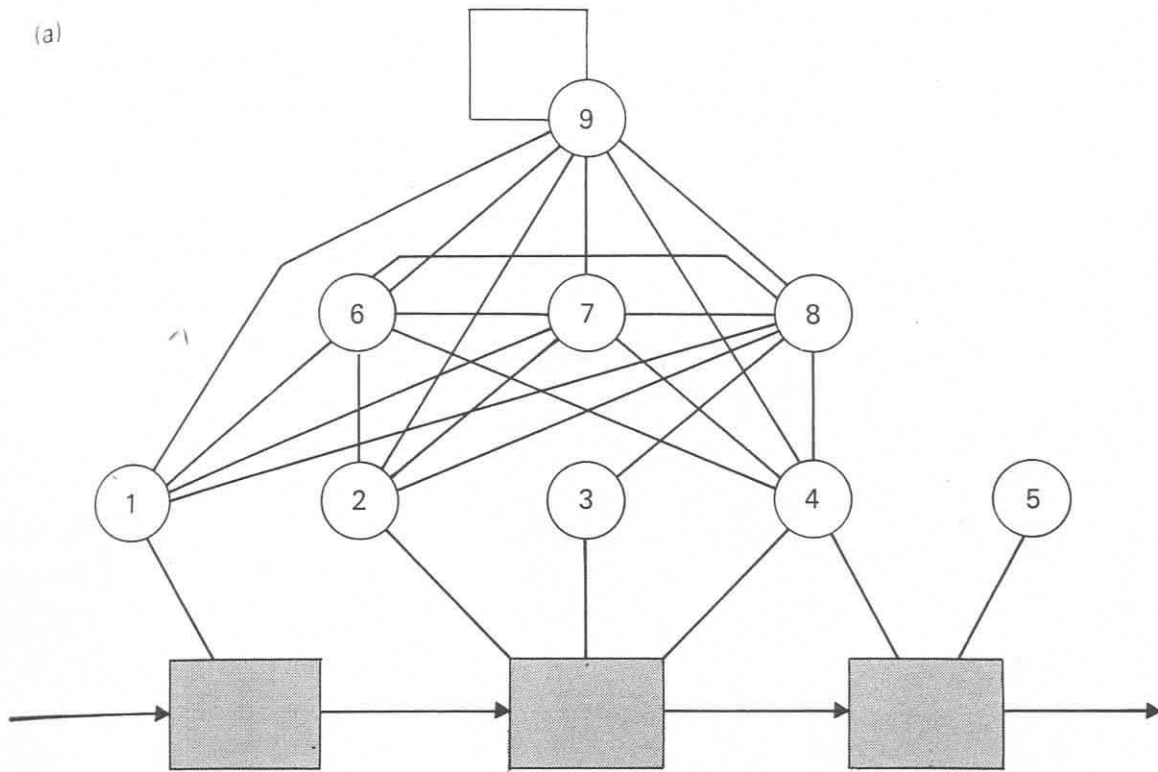
Two major chunks of theory can each account for several, but not all, food web patterns. One focuses upon dynamic interactions between species, the other on simple, static assembly rules in which body size appears to play an important part. Both also have to compete with an untidy group of 'natural history' constraints that may also explain an important subset of patterns. On present evidence no one theory or group of theories can claim precedence over any other as the best or most general explanation for structure in food webs.

In trying to understand the likely relative contributions of these conflicting explanations, we need to remember one simple fact. The quality of the published data is so variable and idiosyncratic, and so highly skewed in the direction of 'poor' on a scale from awful to excellent (Cohen 1978; McCormick & Polis 1982; Pimm 1982; May 1983; Paine 1983, 1988; Cohen & Newman 1985; and many others) that several of the patterns may eventually prove to be artefacts. As we have already noted (p. 45), many 'species' are in fact aggregations of various taxa. Equally serious are major variations in the spatial and temporal scales over which data have been gathered. Figures 3.1 and 3.2 show how the perceived structure of two food webs changes with increasing spatial and/or temporal investigation (Kitching 1987; P. H. Warren, personal communication). These data speak for themselves.

Worries about artificial patterns aside, the poor quality of the data also implies that explanations for perceived patterns must be very simple. It defies logic to suggest that the motley collections of binary links identified by sampling food webs in nature with varying degrees of efficiency are all dynamically important, or that dynamics alone explain the structure of any particular web. However, providing only that real predators take prey smaller than themselves (or parasites attack hosts bigger than themselves), the cascade model should accurately predict

FIG. 3.1 Several versions of the same food web for animals inhabiting water-filled tree holes in south-east Queensland (from Kitching 1987). (a) shows the full regional web, based on all sampling stations and seasons. There are nine taxa in the regional web, indicated by circles 1–9. Feeding links between taxa are indicated by lines. In most cases these links are unambiguous (e.g. 9 feeds on 1, 6, 7, etc.), but it is not possible to identify enemies and victims with certainty for some of the links in Kitching's original diagram (e.g. it is unclear whether 6 feeds on 7, and/or 7 feeds on 6); fortunately these details are not important in the present context. The 'square' on species 9 indicates that it is cannibalistic. (b) and (c) show webs at particular sites on particular sampling occasions. The positions of particular species in (a)–(c) are constant, so that the missing components in (b) and (c) are easily identified. The base of the food chain in these tree holes is detritus; the boxes at the base trace the breakdown of detritus particles. The perceived structure of the food web varies with the temporal and spatial scale of sampling.

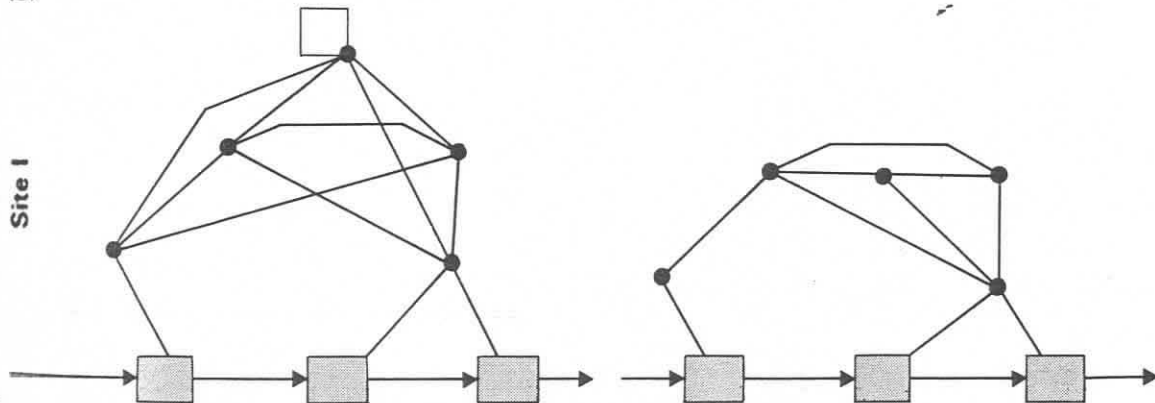
(a)



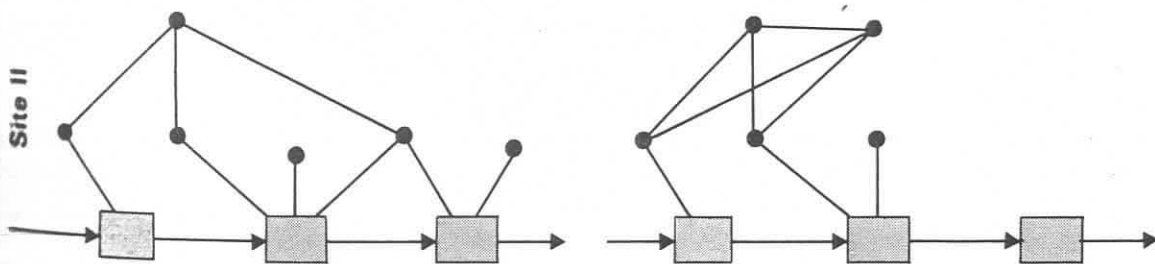
(b)

Time period 1

Time period 4



(c)



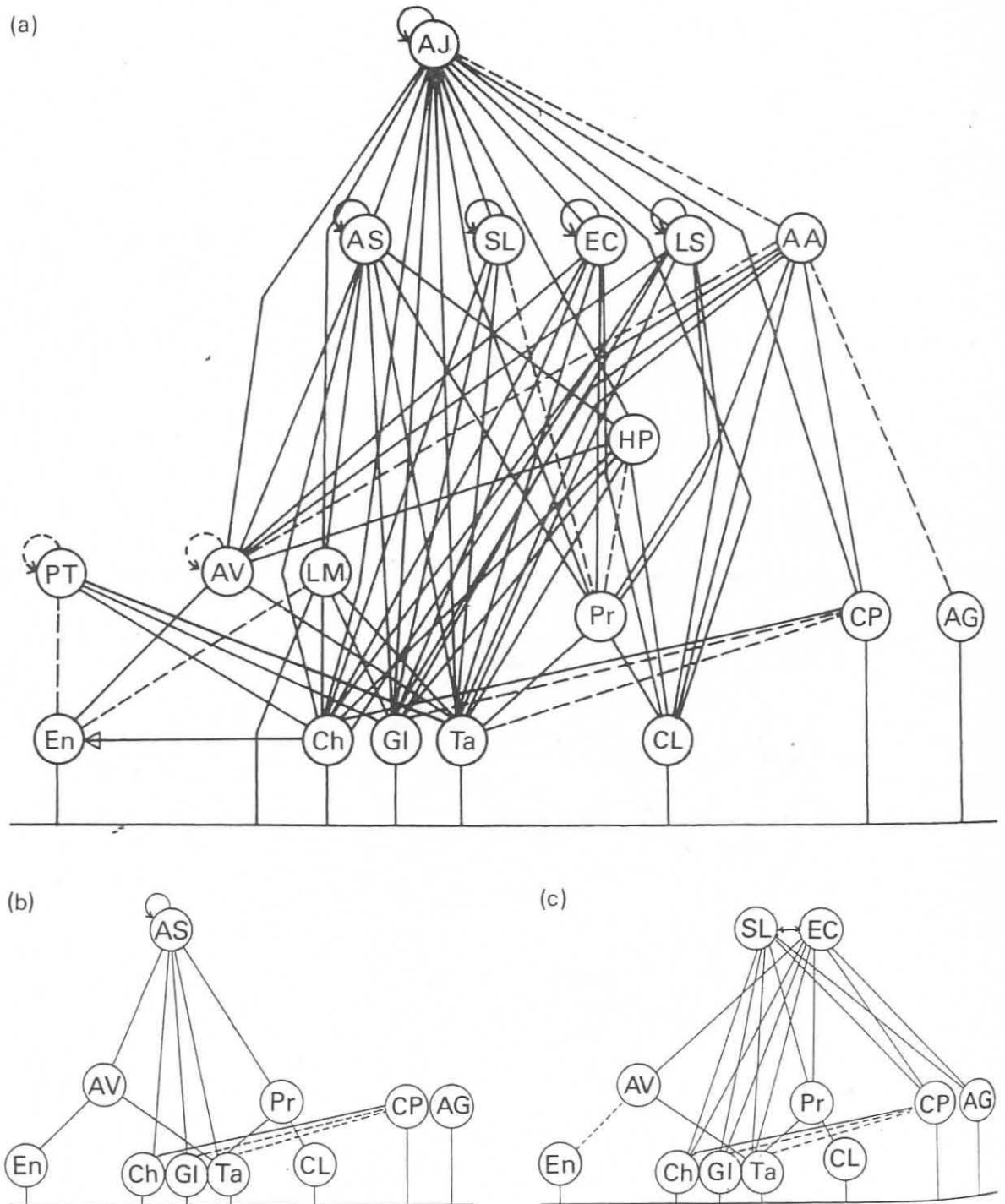


FIG. 3.2. Three versions of the same food web for animals inhabiting an acid pond at Skipwith Common, North Yorkshire (P.H. Warren, personal communication). (a) shows the full web at the weedy margin of the pond, based on all sampling dates. Also shown are webs for the open water in spring 1986 (b) and spring 1987 (c). No species occur in the open water that do not also occur at the margins. The positions of particular species, together with their coded identities, are the same in (a)–(c), so that the missing components in (b) and (c) are easily identified. Dotted lines represent probable links. Cannibalism is indicated by a small loop from each species back to itself. All links are from victims to predators at higher positions in the web, except for the link between SL and EC in (c), where each species preys on the other. As in Fig. 3.1, the structure of the food web varies spatially and temporally.

structure in the crudest data imaginable. My intuition therefore says that several of the patterns in published food webs are generated by the cascade model, with species body sizes acting as the key, organizing variable. In other words, Elton got it more or less right.

Where does this leave predictions based on dynamic models? Undoubtedly there are strong interactions in food webs, and for this subset, Lotka-Valterra models may make the right predictions for more or less the right reasons. Both static and dynamic processes then march together to yield observed patterns. [Parenthetically, note that it would be interesting to construct dynamic models of food webs explicitly incorporating species of a range of sizes, with the parameters scaled accordingly, e.g. Peters (1983)]. In comparing dynamic models and the cascade model, notice also that the density of links per species (pattern ii on p. 46) must be fixed at observed levels before the cascade model yields the right answers. It is far from clear why each species in a food web should, on average, feed on the same number of other species, irrespective of the number of potential victim species (May 1986; Warren & Lawton 1987). Elementary biological constraints must often restrict species' diets, but is it as simple as that? Too much connectance destabilizes model food webs (p. 50), and hence may impose limits on connectance in the real world. If so, a key parameter in the 'static' cascade model may be a product of dynamic interactions between species. A pioneering theoretical attack on this problem is provided by Cohen & Newman (1988). Of course, these are highly speculative arguments. If nothing else, they serve to remind us how little we still know about the structure of species assemblages.

As the quotations in the Introduction make plain, Elton believed that several processes contributed to the structure of food webs. Sixty years on, Table 3.1 suggests that he was correct. The effects of body size are clearly important, but they are unlikely to be the only processes involved. The spotlight must now focus on the relative contributions of static assembly, body size, dynamics, energy flow and natural history, as they meld to create patterns in the food cycle.

WHERE NEXT ?

I cannot see that ecologists have much more to learn from staring even harder at the compendium of published webs. As Paine (1988) points out: '... these qualitative descriptions were never intended to be data, to serve as fundamental grist for the theoretician's mill'. Fortunately, I sense a growing interest in gathering more and better data, in doing experiments on food webs, and in thinking about new approaches to understanding their structure.

In an ideal world, what form should new data take? In no particular order, the spatial and temporal extent of each study must be defined, and the criteria for specifying that A feeds on B need to be explicit; the probability of discovering a feeding link depends on sampling effort; for example (Cohen 1978). We should avoid lumping taxa; species identities need to remain intact. At very least, such data would allow us to be confident that the patterns so far documented are real, and not artefacts. Not everybody agrees that all, or even a majority of the patterns in Table 3.1 are reliable; others, myself included think that they are sufficiently simple and robust to be worth studying, despite the data. But I would feel happier if I had more confidence in the basic information. Several recent studies stand out as models for others to follow (e.g. Beaver 1983, 1985; Hawkins & Goeden 1984; Hildrew, Townsend & Hasham 1985; Kitching & Pimm 1985; Sprules & Bowerman 1988).

No less important or interesting would be different sorts of information. Elton (1927) drew up a hypothetical food web involving predators and parasites, and shrewdly observed that food chains might be very long when traced through mixtures of both sorts of enemies, because body size constraints are relaxed. More generally, energetic or dynamic constraints should still operate in real webs that include predators, parasites and diseases, but the distribution of feeding links is unlikely to be upper triangular, violating the cascade model. Yet despite Elton's early insight, students of food webs have studiously ignored parasites and diseases (May 1983; Price *et al.* 1986), a few have studied parasitoids, and nobody has combined all classes of 'enemies' into a study of a single web. Because such 'mixed' food webs seem to offer an opportunity to tease apart the relative contributions of dynamic and static processes, they deserve immediate attention.

Ecologists have also been slow to study and model at one and the same time the full cycle of trophic links, embracing not only plants, herbivores, predators and so on, but also corpses and decomposers. The 'national anthem' of my adopted county of Yorkshire ('On Ilkley Moor baht'at') reminds us that loops in food chains are commonplace if we include decomposers in our thinking (the song specifically identifies the pathway from humans, worms, ducks and back to humans); at least superficially, such loops do not appear to be destabilizing. Indeed, a number of recently discovered and fascinating trophic interactions have yet to feature in empirical and theoretical analyses of food webs (e.g. Hanski 1987). At least 25%, sometimes more, of the net primary production of planktonic algae may appear as dissolved organic matter (DOM) in marine ecosystems (Kurihara & Kikkawa 1986). DOM is taken up and

used by bacteria, which in turn are consumed by heterotrophic flagellates. Both bacteria and flagellates serve as food for consumers that also double up as 'normal' primary consumers of algae (Azam *et al.* 1983; Fenchel 1986, 1987). The 'microbial loop' adds considerable complexity, not to say several more steps, to planktonic food chains. Some freshwater food webs, particularly those in humic lakes, may also support hitherto unexpected links via DOM, heterotrophic flagellates and zooplankton (Salonen & Hammer 1986). Equally intriguing for the light they might shed on the processes structuring food webs would be detailed studies of other unconventional trophic links: planktonic ciliates that store chloroplasts from algae, and which therefore live double lives as grazers and primary producers (Hanski 1987), and insectivorous plants in terrestrial and freshwater communities that turn the tables on animals and act as predators. Mutualists and symbionts might also be usefully and routinely incorporated into our studies whenever and wherever there is exchange of energy between them.

It is unclear to me what predictions dynamic models might make about permitted structures in food webs containing these and other unconventional or at least poorly studied trophic links. If they turn out to be clearly different from food web structures expected under alternative models, they may throw a chink of light on the conflicting explanations summarized in Table 3.1.

Such questions aside, several major and more radical initiatives suggest themselves. Paine (1980, 1983) has been virtually alone in arguing that not only the presence, but also the strength of feeding links needs to be investigated, and has pioneered the use of manipulative field experiments to distinguish between strong and feeble interactions in intertidal food webs (e.g. Paine 1966, 1971, 1980). An apparent lack of compartments or 'modules' in food webs could conceivably be an artefact of using binary data (Paine 1980; Pimm & Lawton 1980). If strong interactions are grouped in some way, it has important theoretical implications for community stability (May 1979; O'Neill *et al.* 1986; and references therein). A second, related theme already touched on, is that much more thought needs to be given to spatial and temporal scales of study. Food webs in nature are nested in time and space (Harris 1985; O'Neill *et al.* 1986). Current investigations simply break into this hierarchy at arbitrary points. For sound practical reasons, an investigator may choose to focus on insect herbivores, parasitoids and predators on one or more species of food plants in a small area. Or he may choose to paint a bigger picture on a larger canvas incorporating deer, rabbits, foxes and eagles, and ignore or roughly sketch the insignificant insects. But

what we actually have are a series of webs made up of small organisms, with short generation times, interacting over small spatial scales, embedded within food chains of progressively larger, longer-lived and more widely ranging beasts. This hierarchical structure may profoundly influence the way in which ecosystems work (Harris 1985; O'Neill *et al.* 1986), as well as making it more difficult for biologists to understand how they work. As Harris (1985) succinctly points out: 'a reductionist approach using simple equations (suitable for small number systems) cannot represent the hierarchical and emergent behaviour of a loosely nested middle number system.' ('Small number' systems are tractable sets of three or four species; 'large number' systems have emergent statistical properties typified by the gas laws; for better or worse, students of real food webs and communities are stuck with 'middle number' systems.)

Third, and again related, what are the principal mechanisms that filter species out from a regional pool of potential food web members, and determine who feeds where and when? (Beaver 1983, 1985; Kitching 1987; see also related discussions in Ricklefs 1987). Presumably, chance dispersal, environmental conditions and species interactions all play a part, but how do they combine to create local webs? Beaver's (1983) work on the food webs of *Nepenthes* pitcher plants in South East Asia illustrates the nature of the processes involved.

There is considerable variation between individual pitchers in insect species composition, even after the effects of pitcher age have been eliminated. At the level of the individual pitcher, chance processes and the recent past history of the patch probably play an important role in the determination of which species are available to colonise a pitcher when it first opens. There may be priority effects, probably usually mediated through intra- or interspecific competition for food. . . . The presence of predator larvae will also affect the faunal composition . . . The community within an (individual) pitcher can never reach equilibrium. At the level of the patch of *Nepenthes* pitchers, greater stability is possible.

Or consider the more specific question, touched on in this quotation from Beaver. How important are trophic interactions involving polyphagous enemies in excluding species from particular habitats and food webs — so called competition for 'enemy-free space' (Jeffries & Lawton 1984; Lawton 1986b; Mithen & Lawton 1986), or 'apparent competition' (Holt 1977, 1987)? Paradoxically, notice that because apparent competition implies that polyphagous enemies sustained by alternative prey totally eliminate particularly vulnerable victims, some of the most interesting and potent feeding links in food webs may be ones that are no longer there to investigate!

Overlapping with all that has been said up to this point is the need not only to observe and to describe food webs, but to manipulate them. Pimm & Kitching (1987) show what can be done, particularly in small

aquatic communities. I would like to see many more experiments that vary habitat productivity, predictability and structure (to name but three possibilities), and then monitor what happens to food web structure. Finally, theoretical and empirical studies all make the obvious point that food webs are about more than just energy transfer. Crucial species interactions may involve exchange and cycling of limiting nutrients, for example amongst mutualists, or between plants, micro-organisms and detritus. These vital links between species are not represented in the gallery of published webs. Moreover, trophic interactions (broadly defined) are themselves played out against a background that also involves competitive contests between species. General models of community assembly usually embrace all classes of species interactions (e.g. May 1973; Lawton 1987a). Some attempt has been made to allow for them in empirical studies of food webs (e.g. Rejmanek & Sary 1979; Briand 1983); but a widespread failure properly to quantify and simultaneously study predator-prey, competitive and mutualistic links in communities significantly weakens the bonds between theory and empirical studies.

CAN IT BE DONE ?

It is embarrassingly easy to list ways in which existing empirical data on food webs could be improved, and depressingly difficult to see how to achieve these high ideals in practice. Food web studies highlight a crucial problem that confronts all areas of ecology (Lawton 1987b). There is no shortage of important theoretical ideas about how populations are regulated, or how communities of living things are put together, or about many other ecological phenomena. To test these ideas, to refine them, refute and build better hypotheses, ecologists need more than anything else teams of people, sets of willing and skilled hands to do field manipulation experiments, or to sort, identify, weigh, grind up and so on. It is trite, but true that most of the ideas outlined above are Herculean tasks that cannot be solved without great labour; there are no sophisticated machines costing millions of pounds to do the job for us. Yet precisely because a great deal of important ecology cannot be done with very expensive electronic wizardry, it is too often seen as 'soft science', not to be taken too seriously. The irony is that we now know far more about black holes and distant galaxies than we do about the communities of living organisms that make up the life-support systems of our own planet. Food webs provide a touchstone in our efforts to discern and then understand patterns in nature. Sixty years down the road pioneered by Charles Elton, ecology stands at a crossroads. Unless we can win a share

of resources more equal to the tasks that confront us, progress over the next 60 years will be painfully slow. By then, many of the world's most exciting ecosystems may have been lost for ever, and with them our last chance to understand how they work.

ACKNOWLEDGMENTS

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